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THE ARCHEGONIUM OF MNIUM CUSPIDATUM.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. LIII.

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(WITH PLATES V AND VI)

ALTHOUGH the archegonium of mosses has been much studied, the origin of the axial row and the relationships of the various members comprising it have been left in uncertainty. These points can be established best by mitotic figures, but mitosis in mosses must go on very rapidly, for figures are rare; and it is no doubt due to the infrequent observation of mitotic figures that these questions have been left so long in uncertainty and that observers have been led to different views.

For the present work material was collected at the Dalles of the Wisconsin River in Wisconsin, along the Missisisippi River in upper Iowa, near Oberlin in Ohio, at Starved Rock and in the vicinity of Chicago in Illinois. The methods used were those that have been generally approved. Since the terminology used in the various papers dealing with this subject is confusing, it may be stated that that used in this paper is largely that of Janczewski (9).

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HISTORICAL.

In 1851 Hofmeister (1) outlined the development of archegonia and antheridia in bryophytes, showing that the earliest stages of both are identical, a fact fully confirmed in the present paper; but his view as to the origin of the axial row in the archegonium and of a similar row in the antheridium receives no confirmation.

Schimper (2), in studying Sphagnum, confirmed Hofmeister's account of the early stages of the archegonium, but did not commit himself in reference to the origin of the axial row.

Leitgeb (5), in examining a few plants of Sphagnum, found a single archegonium in each, directly arising in each case from the apical cell, the first division being transverse.

Kühn (8) investigated Andreaea, and discovered similarity in the very earliest stages of archegonia and antheridia, but outlined the further development of the two organs very much as they are ordinarily understood today.

In 1872 Janczewski's paper (9) appeared, and his conclusions that concern this paper are as follows: The first divisions of the archegonium initial are exactly the same as those of the antheridium, and at this stage the two organs are not distinguishable. The cover cell does not remain inactive, but produces adventitious segments (not exceeding six) and canal initials. The inner cell (the first cell cut from the lower end of the terminal cell) divides to form the central cell and the primary canal initial, and the central cell produces the egg and ventral canal cell. The canal cells have different origins; the lower arising through transverse divisions of the primary canal initials, the remainder through the divisions of the adventitious cells.

Hy (12) in an extensive review of researches on the archegonium supports the views of Janczewski.

In 1895 Campbell (13) gives a detailed account of the development of the archegonium in *Funaria hygrometrica*, agreeing very nearly with that of Kühn for Andreaea. The cover cell acts as an apical cell, cutting off four rows of segments, three from the lateral faces to form neck cells and one from the base to form the axial canal row. The lateral segments divide by vertical walls, making six peripheral cells which later divide by transverse walls; but the canal cells, so far as could be determined, do not divide after they are first formed.

In 1897 Gayet (15) published observations on the development of archegonia in twenty-two genera of mosses and liverworts. His conclusions differ at two critical points from those of other observers, namely the origin of the axial row and the similarity of archegonial development in liverworts and mosses.

He finds that the archegonium in liverworts exhibits both intercalary and terminal growth; that in mosses this terminal growth contributes notably to the length of the organ, five or six adventitious segments being formed at the expense of the apical cell; that the terminal cell does not contribute at all to the canal cells, either in mosses or liverworts; that the neck canal cells all arise from an initial cut from the mother cell of the egg; that two ventral canal cells are occasionally found in Sphaerocarpus, and one such case was noted in Marchantia; and that the ventral canal cell in Marchantia is capable in rare cases of being fertilized in place of the egg.

Goebel (18), having examined the development of archegonia in *Mnium undulatum*, is unable to sustain Gayet's views, but corroborates those of Kühn, Janczewski, and Campbell, namely that the moss archegonium develops in part by segments (some of which are axial) cut from an apical cell; and in this regard is to be distinguished from the liverwort archegonium with its inactive cover cell.

EARLY STAGES OF THE ARCHEGONIUM.

In early stages archegonia and antheridia cannot be distinguished. Enlarged papilliform cells arise from the surface of the receptacle, and segments are cut off right and left from a two-sided apical cell (*figs. 1–10*). This method, just as characteristic for archegonia as for antheridia, agrees with Hofmeister's account (1), but differs from the accounts of Leitgeb (4), Kühn (8), Janczewski (9), Campbell (13), Gayet (15), and Goebel (18) in the absence of a wall that cuts off a basal cell from the archegonium initial or the archegonium mother-cell. When six to eight segments have been cut off, the two-sided apical cell is transformed into a three-sided one, a process that introduces a history distinctly characteristic of the archegonium.

The first indication of this change that marks the organ as an archegonium is seen in a division of the apical cell which results in the introduction of a curved wall more nearly vertical than that which cuts off any preceding segment. The approximately vertical position of this wall causes it to fall upon the same wall below as that which the wall immediately preceding joins (*figs.*

11, *12*). This ends the work of the two-sided apical cell and introduces that of the three-sided one, so characteristic of growing organs in the archegoniates. Leitgeb (4, p. 6) sought some instances of divergence by which this shift from a one-half to a one-third divergence could be explained, but without success. The transition is abrupt and not by gradual stages. The next division of the apical cell is longitudinal and cuts off a tangential segment from a middle cell. It is evident that the introduction of the last three walls constitutes the beginning of the archegonium proper, and the middle cell the beginning of the canal. All that lies below this constitutes the pedicel, which in mosses comes to be very massive (*figs. 14*, *19*, *25*, *28*) and often very long (*figs. 16*, *20*, *45*, *47*).

While the divisions of the apical cell have been in progress, transverse and longitudinal divisions have been taking place in the segments below (*fig. 12*), only two or three of the lowest segments not being thus divided (*fig. 12*), and the transverse divisions generally appearing first (*fig. 7*). Longitudinal divisions occur in the three peripheral cells, producing a neck of seven cells, a middle cell surrounded by six peripheral cells (*fig. 48*, *c*, *d*). The middle cell next divides transversely, producing a terminal cell (*t*) and an inner cell (*i*) (*figs. 13*, *14*, *18*). There is no dissent from the view that this inner cell in both mosses and liverworts is the first of the axial row and a progenitor of the egg. It divides transversely, giving rise to the central cell (*c*) (*figs. 15*, *16*, *19*, *22*) and the primary canal initial (*p*) (*figs. 19*, *22*). The central cell does not divide again until the division which gives rise to the egg and ventral canal cell, gradually increasing in size until its volume is six or eight times that of the neck cell lying next to it (*figs. 24*, *33*). The primary canal initial, on the other hand, soon divides, and with the subsequent divisions of its daughter cells helps to form the canal series. It will be seen that the development thus far is practically that of the archegonium in liverworts.[1]

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[1] Compare Leitgeb (10), Kny (3), Janczewski (9, p. 402), Strasburger (6 and 7), and other observers who deal with liverworts.

THE TERMINAL CELL AND THE CANAL CELLS.

The most difficult part of the research is to determine the behavior of the terminal cell and that of the canal cells from this period. That the origin of the axial row, including the points just mentioned, is a difficult problem is evident from the conflicting accounts of those who have attempted to solve it. There is quite general agreement, however, that the terminal cell in the mosses does not cease activity after cutting off the primary peripheral cells and the inner cell, as does the cover cell in the liverworts, but continues to increase the length of the archegonium neck by cutting successive peripheral segments from its three lateral faces.

The status of the problem of the origin of the canal series may be summarized as follows: Hofmeister's (**1**) idea that the canal series arises from one of the four original pedicel rows as triangular tangential segments of its cells is mentioned only as a matter of history, the erroneous conception soon being abandoned; Kühn (**8**, p. 31) claims that all the cells of the axial row are cut from the base of the apical cell (*cf.* his diagram, *pl. 10, fig. 71*); Janczewski (**9**, pp. 412, 413) says that the numerous canal cells are of diverse origins, the lower arising through transverse divisions of segments cut from the base of the apical cell; Campbell (**13**, p. 19) says that the segments cut from the base of the apical cell constitute the axial row of neck canal cells, which, so far as could be determined, do not divide after they are first formed; according to Gayet (**15**, p. 241), all the neck canal cells have the same origin, all arising from an initial cut from the mother-cell of the oosphere, and no segments being cut from the base of the terminal cell; and finally Goebel (**18**, p. 244) holds that the moss archegonium is distinguished from that of the liverwort by its characteristic growth from an apical cell, which also contributes canal cells, figuring such a cell in a row of twenty canal cells.

Three sources are thus alleged for the canal cells: (1) the apical cell with intercalary additions; (2) the apical cell alone; (3) not the apical cell at all, but one at the opposite end of the row. Gayet alone holds the process to be like that in the liverworts; the others declare it to be peculiar to mosses. In the full accounts some authors state that this process of basal segment cutting ceases very early; one that it continues late in the growth of the archegonium; and a third implies this, though it is not stated. The disagreement as to time is thus as evident as the disagreement as to method.

It may be argued that the disagreement in these conclusions is to be accounted for by the fact that they are drawn from observations on different forms; yet it would seem that such a process in closely related forms would not be radically different. There seems to be no alternative but to examine the development of the archegonium in a sufficient number of forms to discover whether there is any such thing as general agreement, and as a contribution to this the record of events in *Mnium cuspidatum* is here presented.

In this species the terminal cell continues to cut off successive peripheral segments laterally (*figs. 13–20, 24, 30, 34, 37*), and these increase the length of the archegonium neck. Transverse divisions in the peripheral cells and in the canal cells go on simultaneously (*fig. 15*). The presence of mitotic figures in the same phase side by side in the two rows leaves no room for doubt on this point, and establishes the fact that part of the growth in length of both neck and canal is intercalary. The terminal cell now cuts off a second cell from the lower face. This statement rests on the presence of the mitotic figure shown in *fig. 20*. The search for a figure in this particular cell was a long one, and its value should not be underestimated, for it proves that the terminal cell contributes to the growth of the axial row. The process would seem to be unique, differentiating the mosses from all other archegoniates in this particular.

In this connection it may be stated that careful search was made in the literature bearing upon this and related points for confirmatory evidence of the relationships of the members of the axial row based on the presence of mitotic figures, but no such evidence was found. Hundreds of figures illustrating all stages of archegonial development in both mosses and liverworts were examined, but in none of them are spindles shown. Conclusions in all cases seem to have been reached without the sure evidence of the mitotic figure.

Having shown thus that some cells are added to the axial row by segments cut from the lower face of the terminal cell, it must next be determined whether all or only part of the remainder are thus formed, intercalary divisions being the alternative. Here too the evidence of the mitotic figures will be appreciated, for if found in the row intercalary growth can hardly be questioned. Fortunately these were found, and four such cases are shown (*figs. 24, 31–33*), proving that there are additions to the row by intercalary divisions.

How long the terminal cell continues to act as an apical cell, and whether the cutting off of canal cells ceases before the cutting off of peripheral cells are questions to be asked at this point. The number of cells constituting the row is variable. That the cutting off of cells from the lower face of the terminal cell ceases early, in some cases at least, is evident from *figs. 24, 32, 33*. Here a longitudinal wall through the center of each terminal cell clearly prevents any further additions to the axial row from this source. The presence of such a wall in the terminal cell when the number of cells composing the row was only eight or ten is very common; that in *fig. 24* is exceptionally early. There is no evidence to show that addition to the row from the terminal cell continues in any archegonium later than the age indicated in *figs. 32–34*, and much to show that it does not. Goebel (18, p. 244, *fig. 138*, IV) reports one case where such a division has occurred in a row of eighteen or more cells, but the absence of a mitotic figure leaves some room for question.

On the other hand, the production of neck cells by the terminal cell continues till late in the development of the archegonium, but the last divisions for this purpose are always intercalary (*fig. 30*). In many cases the number of cells in the axial row is noticeably less than those in the peripheral rows which inclose the canal row. There does not appear to be any relation between neck rows and canal row in this regard, for in other cases the numbers are nearly equal, and in a few cases those of the neck rows were less than those of the axial row.

THE DIVISION OF THE CENTRAL CELL.

The division of the central cell results in many cases in two cells of nearly equal size. This is well illustrated in *figs. 26–29*, in which the ventral canal cell is nearly as large as the egg. This character strengthens the view that the difference in size and function of the egg and ventral canal cell may not always have existed. In fact, an equality in size and probably in function may reasonably be regarded as a primitive condition; and the existing inequality may be regarded as a specialization, which among pteridophytes and gymnosperms has led to a gradual reduction in the relative size of the ventral canal cell, then to the disappearance of the wall separating its nucleus from that of the egg, and finally to the entire disappearance of any vestige of the cell. Goebel (18, p. 242) refers to this approximate equality in size of egg and ventral canal cell in the bryophytes, saying that they are nearly equal in many cases, but that in most cases the egg is larger. He admits that the meaning of this division is not known, but since the ventral canal cell is always present, he is inclined to believe that it has some physiological rôle, and suggests the separation of the chemotactic substance for the attraction of the sperms as a probable function.

The division of the central cell is comparatively late. No case was found where division occurred before a row of seven cells had been formed (*fig. 34*), and very often eight or ten (*figs. 32, 33*). No mitotic figures for this division were found, but the position of the nuclei and the septum, and other features, are such as to leave no doubt whatever concerning the relations of these two cells. A wall separating egg and ventral canal is always present for some time after the division takes place, but not infrequently it disappeared while the remaining septa of the row were still intact.

TRANSVERSE SECTIONS OF THE ARCHEGONIUM.

All the evidence for the development of the archegonium thus far presented has been drawn from longitudinal sections. Several series of cross-sections were made, two of which are presented herewith, and from them the following conclusions are drawn: (1) The terminal cell is triangular in cross-section, inclosed by three peripheral cells which have been cut from it successively (*figs. 48, b, 49, a*). No mitotic figures were found, but the position of the walls and nuclei indicate their origin, (2) The three peripheral cells divide longitudinally and produce a neck of seven rows—six peripheral and one central (*fig. 48, c, d*). These divisions are not simultaneous (*fig. 49, a*) and appear early, for the neck has six peripheral cells at the level of the second nucleus, less than 0.5^{mm} from the apex (*fig. 48, c*). (3) The neck has two peripheral layers near the venter (*fig. 48, j*). (4) The canal is hexagonal in outline and maintains this character till the egg is formed (*fig. 48, i*), and the venter wall breaks up into many cells (*fig. 49, g*). (5) Certain large cells, lying just below the egg and having the appearance in longitudinal sections of being members of the row (*figs. 26, 27*), are found here also, but are clearly no part of the row (*fig. 48, k, l*). (6) The pedicel bears throughout its length the quadrant character given to it by the early longitudinal divisions of the pedicel segments. Beginning at the base, the development upward is through quadrant, octant, and intermediate stages to the base of the archegonium proper, where the pedicel is twelve-celled in cross-section. At this point each quadrant consists of a center cell and two peripheral cells (*fig. 49, g–k*).

THE PERIPHERAL CELLS.

From the mode of origin of the neck of an archegonium of six rows, as already described (*fig. 48, c, d*), it is evident that the cells forming any row do not stand directly over one another, but alternate spirally around it, since they are cut off successively around the apex (*cf.* Janczewski, **9**, p. 409). The longitudinal divisions which produce the six neck cells are usually followed by two or more transverse divisions in each cell, giving rise to vertical groups of four (*fig. 23*). In the early pedicel segments only one division occurs, and in some of the later segments division occurs in only one of the two cells arising from the first division, giving rise in such cases to groups of only two or three cells. The axes of these groups come later to stand in an oblique direction (*fig. 23*).

It is well known that as the archegonium approaches maturity there is usually more or less torsion of the neck. I am disposed to attribute this torsion to the alternating arrangement of the peripheral cells as a disposing cause, if not the efficient cause. Janczewski (**9**) noticed both the alternation (p. 408) and the torsion (p. 410), but did not relate them. Campbell (**13**, p. 194) calls attention to the fact that the rows are not vertical, but says that the neck cells do not stand in vertical rows, but are somewhat obliquely placed owing to the torsion of the neck during its elongation. This explanation would account for the cells not being in vertical rows, but leaves out the fact that the cells never were in vertical rows, but in oblique rows from the first, owing to the way in which they were cut from the terminal cell. A study of *fig. 19* will show that as the cells composing each group lengthen in their growth torsion must be inevitable.

THE HOMOLOGY OF ARCHEGONIA AND ANTHERIDIA.

The question of homology of archegonia and antheridia is not new. Homologies in the development of male and female sex organs and of the gametes themselves among the lower forms are well established, as mentioned by Goebel (**18**, p. 243). This has been a more difficult problem for organs as stable as archegonia and antheridia. The archegonium is highly differentiated, but maintains its form and other characters so constantly that it serves as the important structure in establishing the natural relationships of several great groups of plants. It is so different in form and function from the antheridium that attempts to homologize the two organs on general features have not been successful. Goebel (*l. c.*) admits that in the mosses very great differences in structure of the sex organs exist from the very beginning of their development, and thus implies the difficulties that lie in the way of homologizing these organs. I shall attempt to establish the homology of archegonia and antheridia by showing the homology (1) of the early stages, (2) of the cells of the axial row, and (3) of the axial row series and sperm mother-cells.

1. *Homology of early stages.*—Both organs start from papilliform superficial initials, increase in length through the alternate

divisions of a two-sided apical cell, and from these early segments a pedicel is formed. From the cells supported by the pedicels arise the sterile external wall of the gametangium, and the fertile gamete mother-cell tissue inclosed by the wall. Both organs are closed while developing, but organize special regions in which apertures appear at maturity.

2. *The homology of the axial row series.*—That the cells composing the axial row constitute a homologous series is indicated by development of the row. In the first place, egg, ventral canal cell, and neck canal cells are all closely related in origin. They are all the progeny of either a single cell cut from the truncate apex of the terminal cell (Riccia), or of such a cell and subsequent cells cut from the same region in identically the same way as the first (Musci). Again, egg and ventral canal cell are sister cells, and at the time of formation are not widely different in size or appearance (*figs. 26, 28, 29*). It appears possible even that the ventral canal cell or the lowest canal cell may function as the egg.

The theory that the ventral canal cell is an abortive egg is strongly supported by Chamberlain's account of Pinus (**17**), in which the ventral canal cell is occasionally organized as an egg and in rare cases may function as such. Ikeno (**19**) from a study of Ginkgo, and Land (**21**) from his study of Thuja have arrived at similar conclusions. Gayet (**15**) reports an instance in Marchantia where the ventral canal cell was fertilized instead of the egg, but unfortunately the specimen was not saved, nor was a figure made. My own observations on Mnium yielded a case in which the ventral canal cell had outstripped the egg in growth (*fig. 42*), and doubtless would have been fertilized in place of the egg. It is possible in cases of this nature (*fig. 42*) that the larger of the two cells may be the lowest cell of the canal row and would later have given rise to a ventral canal cell and an egg.

Another unusual case which supports this homology is seen in *fig. 43*. Here there are two eggs each with its own ventral canal cell. There can hardly be any doubt that either or both of these eggs could have functioned and produced embryos, had fertilization taken place. There are two ways in which this phenomenon can be accounted for: first, the central cell may have divided very early, giving rise to two central cells, each of which later divided and gave rise to an egg and ventral canal cell; second, the lowest canal initial may have acted as a central cell, producing by its division an egg and ventral canal cell. Coker (**22**, p. 137) has reported and figured a similar case in Mnium, and regards the supernumerary egg as derived from the lower neck canal cell. The absence of septa is to be noted in each instance, a condition not infrequent in gymnosperms.

Campbell (**14**) figures an archegonium of Geothallus which apparently had cut off successively two ventral canal cells, and there is no wall separating the second cell from the egg. There is here the possibility that the two ventral canal cells may be the result of a division of the original ventral canal cell instead of successive divisions of the egg. This view is suggested by the position of the nuclei of the ventral canal cells, both of which are in contact with the septum.

We are disposed to attribute the vigor and consequent supremacy and potency of the egg in bryophytes, just as we do that of the lowest megaspore in angiosperms, to the advantages of nutrition, that is, it is the cell nearest the source of supply. It would be an interesting problem to determine whether by nourishing the canal cells and starving the egg the former could be made to assume the function of the latter. *Figs. 42* and *43*, as also the case in Marchantia noted, seem to suggest that they could do so. At least it is clear from the illustrations here given that there is more or less fluctuation in the origin and work of the cells of the row, and that under certain conditions other closely related cells may do the work of the egg. The cases enumerated seem to furnish sufficient evidence to support the view that the cells of the row are homologous.

3. *Homology of the axial series and sperm mother-cells.*—Another line of evidence indicating the homology of archegonia and antheridia is offered by a number of abnormal forms that constitute a series lying between normal archegonia and antheridia. Bisexual organs are by no means rare. That egg and sperms can

develop in the same gametangium (*fig. 40*), which combines the form, structure, and mode of development of the two sex organs, certainly shows a close relationship between the organs which ordinarily produce egg and sperms separately. We have seen how close is the relationship between the members of the axial row. The central cell and the primary canal initial are sister cells; the division of the former produces two sister cells—egg and ventral canal cell—and the division of the latter also produces two sister cells—canal cells. We find, further, that the second pair may with other canal cells divide longitudinally and produce two canal rows (*figs. 35–37*). An organ of this nature, with its egg and ventral canal cell, with its double-walled venter and single walled neck, must still be looked upon as an archegonium, even if it has deviated slightly from the type. But when the canal members break up by successive divisions until we have an organ such as that shown in *fig. 40*, where the canal row is lost in sperm mother-cells; or that in *fig. 45*, where the egg is lost, but other members of the canal series are retained as a row, we can no longer regard the organ as an archegonium, but must look upon the first (*fig. 40*) as a bisexual organ and the second (*fig. 45*) as a modified antheridium. It will be seen that these three forms—modified archegonium (*fig. 37*), bisexual organ (*fig. 40*), and modified antheridium (*fig. 45*)—constitute a progressive series leading from the normal archegonium to the normal antheridium.

In addition to the abnormal forms already mentioned, two important cases of the apparent conversion of archegonia into antheridia have been reported from different parts of Europe by Lindberg (**11**) and de Bergevin (**20**). In these cases, which are quite similar, a radical change in the life-history of the organs appear. Each organ begins its development with the characters of an archegonium, but closes it bearing the evident characters of an antheridium. De Bergevin gives no sections of the organs, but only a series of external views representing a normal antheridium, an archegonium, and various club-shaped organs leading up to a second antheridium more than twice the length of the first. He speaks of the process as an interconversion of the sex organs. It is doubtful if we should look upon this as a conversion of an archegonium into an antheridium, but rather as the development of a bisexual organ, or a modified antheridium.

These cases seem sufficient to establish the homology of antheridia and archegonia, and point to their derivation from a structure in which eggs and sperms had not yet been differentiated. As an illustration, attention may be called to the fact that in Selaginella the microsporangia and megasporangia are differentiated from primordia which are doubtless indifferent and capable under suitable conditions of producing either kind of sporangium. In this case the microsporangium has deviated less from the structure of the hypothetical sporangium of the homosporous ancestor. Mnium furnishes an illustration of an analogous process, the probably indifferent primordia differentiating into antheridia and archegonia, the antheridia deviating less from the structure of the hypothetical ancestral gametangium. Here, as in Selaginella, the organ which has become most profoundly modified contains vestigial structures which indicate its ancestry and the method by which it has become modified.

THE ORIGIN OF THE ARCHEGONIUM.

The origin of the archegonium and its development into the distinct female organ has never been satisfactorily worked out. There has been some attempt to relate it to the oogonia of Chara or Coleochaete, but no serious claim could now be made for this. To derive the bryophyte antheridium from that of some member of the Chlorophyceae would seem to be a less difficult task.

Barnes (**16**, pp. 277–290) has distinguished between simple and compound spermaries and ovaries, using these terms to designate sperm-producing and egg-producing organs, the simple organs being confined to algae and fungi. The compound spermary could be derived from the simple one by the formation of walls at the time the sperm cells are organized, and by the sterilization of an outer layer of sperm mother-cells for protection. The latter process would be a most natural one in case the plant was forced to change from an aquatic to a terrestrial habitat. In lectures on the bryophytes at the University of Chicago, Barnes has suggested the derivation of the archegonium from some form of primitive compound gametangium. In such a case, by sterilization, a protective wall was secured and the number of gametes greatly reduced, perhaps to a single row as the form took on terrestrial habits. Barnes (**16**, p. 289) regards each member of such a central row as the homologue of a simple ovary. These undergo sterilization from the apex downward, a natural consequence of conditions of nutrition when the eggs are retained in the ovary. Such a process of progressive sterilization would not occur in the antheridium since the formation of a large number of simple sperms is the function, and with this effected the work is done. The egg, on the other hand, must provide for the development of the young sporophyte and requires an abundant store of food for this purpose.

Recently Davis (**23**) has proposed a theory for the origin of the archegonium that has very much in its favor. Because there seems to be no organ among the heterogamous algae from which the archegonium could have arisen, Davis goes to the lower Phaeophyceae for a type to illustrate his views. He takes the asexual plurilocular sporangium of certain Ectocarpaceae as a starting-point. From the asexual zoospores of such an organ sexual gametes arise through differentiation. With sexuality established, the gametangia differentiate until organs are reached from which archegonia and antheridia can be produced by processes already indicated. The aperture at the apex of each organ is significant, and the sterilization of all the gamete mother-cells but one a great advantage to the egg. Davis goes a step further and records that under certain conditions, *Schizomeris Leibleinii* and Draparnaldia have developed zoospores in organs that strikingly resemble plurilocular sporangia; and he is disposed to look upon these structures as forerunners of well-differentiated plurilocular sporangia in the Chlorophyceae.

These views of Barnes and Davis seem to be in the right direction; though it is understood that in any case it is necessary to assume the existence of heterogamous Chlorophyceae of which we have no knowledge at present. Since these views have been advanced considerable evidence in their support has been accumulating, and several cases in Mnium, described in the preceding pages, would seem to support them. The modified organs just discussed (*figs. 36, 37, 45, 46*), and the archegonia taking on antheridial characters in their development reported by Lindberg (**11**) and de Bergevin (**20**), I interpret as indicating that the archegonium is the more specialized of the two organs, and that its atavistic tendency is toward the sporangium-like form and structure of its ancestor. It is natural, since the antheridium is less differentiated, that this atavistic tendency of the archegonium should express itself by first taking on antheridial characters. This it does by its reduced row breaking up again into gamete mother-cells (*fig. 40*); by the neck enlarging (*fig. 40*, also de Bergevin **20**); by its wall tissue becoming chlorophyll-bearing; by the loss of egg and ventral canal cell (*figs. 45, 46*); and by its assuming a general antheridial aspect. A vestige of these processes is also seen in very many archegonia where the expanded apical regions inclose masses of indefinite cells. The explanation offered for the appearance of these expanded apical regions has been that they arose on account of the stretching in a tangential direction of the peripheral cells (Janczewski **9**); but I interpret this as nothing more than an expression in every archegonium of this atavistic tendency. This view of the occasional partial atavism of archegonia expressing itself in antheridial characters bases itself upon the common origin of the two organs from a primitive organ of a sporangial nature, and upon the demonstrated homology of archegonia and antheridia.

SUMMARY.

1. The receptacle is flat-topped with many papilliform cells on its surface, which give rise to archegonia, antheridia, and paraphyses.
2. Archegonia arise from single superficial cells not distinguishable at first from those which give rise to antheridia.
3. The first two divisions of the archegonium initial are oblique and give rise to a two-sided apical cell.
4. The succeeding divisions up to as many as six are from the faces of this two-sided apical cell, archegonia and antheridia agreeing in this regard.

5. Longitudinal radial divisions follow in these segments and form a pedicel of four rows.

6. In the young archegonium the two-sided apical cell gives place to a three-sided one which is truncate.

7. This terminal cell divides transversely soon after its formation, giving rise to the first cell of the axial row.

8. The terminal cell adds to the growth of the neck by segments cut from its three lateral faces, and to the growth of the axial row by segments cut from its truncate face.

9. Growth in length of the archegonium neck is intercalary as well as apical in both the neck and canal rows.

10. The canal series is not always a single straight row, but sometimes double for a greater or less distance.

11. The peripheral cells are not in vertical rows, but alternate with preceding cells; and torsion is a consequence of this feature.

12. The egg and ventral canal cells are often of nearly equal size.

13. The cells of the axial row are homologous with each other and with sperm mother-cells.

14. Archegonia and antheridia are homologous structures throughout.

15. The breaking up of the axial row into sperm mother-cells is an expression of partial atavism on the part of the archegonium.

16. The mass of indefinite cells in the apex of the archegonium neck is the vestige of this atavistic tendency on the part of the archegonium.

17. Archegonia and antheridia probably had a common origin. Hypothetically, the structure from which they have been derived was an asexual multilocular terminal zoosporangium of some primitive extinct member of the Chlorophyceae; the course for the archegonium being through a gametangium possessing more than one functioning gamete.

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EXPLANATION OF PLATES V AND VI.

The figures were all made with an Abbé camera. The lenses used were Bausch and Lomb 1 and 2-inch oculars and $\frac{1}{6}$ objective, and Leitz $\frac{1}{12}$ oil immersion. The plates have been reduced one-half in reproduction, the magnification before reduction being 930, except for *figs. 45–47*.

FIGS. 1–10. Archegonium initial and pedicel segments.

FIG. 1. Papilliform archegonium initial rising above the surface of the receptacle.

FIG. 2. After first division, showing first wall oblique.

FIG. 3. Second wall laid down, forming the two-sided apical cell (*X*).

FIGS. 4–7. Successive stages in ditomic segmentation up to the introduction of the eighth wall; segment cells (*s*) dividing.

FIGS. 8–9. Lateral views of the archegonium initials represented in *figs. 2* and *4*.

FIG. 10. Lateral view of a young archegonium after vertical radial division of the pedicel segments, *cf. fig. 49, p*.

FIGS. 11–22. Showing origin of archegonium mother-cell and other members of the axial row.

FIG. 11. Young archegonium showing first peripheral cell (*r*) cut from archegonium mother-cell (*m*); this division is the first character clearly distinguishing the young archegonium from the young antheridium.

FIG. 12. Young archegonium farther advanced; the archegonium mother-cell (*m*) has divided, giving rise to the terminal cell (*t*) and the inner cell (*i*).

FIG. 13. Young archegonium, lateral view; inner cell (*i*) and second peripheral cell (*r*) cut off.

FIG. 14. Young archegonium; prophase of mitosis in inner cell (*i*).

FIG. 15. Young archegonium; metaphase of mitosis in both the peripheral (*r*) and inner cells (*i*).

FIG. 16. Young archegonium; metaphase of mitosis in inner cell (*i*).

FIG. 17. Young archegonium showing primary canal cell (*p*) and central cell (*c*) resulting from division of the inner cell.

FIG. 18. Young archegonium; same stage as that shown in *fig. 13*.

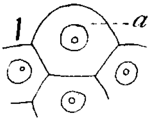
FIG. 19. Young archegonium; same stage as that shown in *fig 17*, but with pedicel farther developed.

FIG. 20. Young archegonium showing mitosis in terminal cell preparatory to cutting off the second canal cell; this feature distinguishes the moss archegonium from all others.

FIG. 21. Young archegonium showing transverse division in a peripheral cell; the section in this region is tangential, not diametral.

FIG. 22. Young archegonium showing increase in size of central cell and progressive work of terminal cell.

FIG. 23. Tangential segment from young archegonium; each peripheral cell has divided once; a second division has occurred in most of resulting cells; torsion of neck probably due to this arrangement of groups.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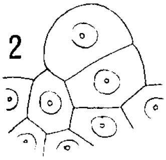
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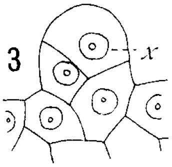
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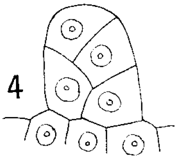
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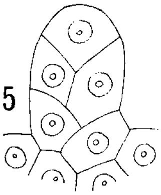
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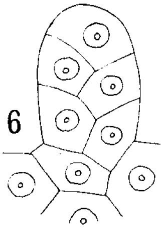
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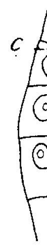
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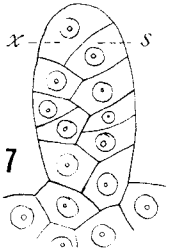
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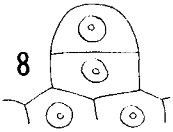
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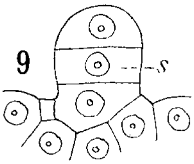
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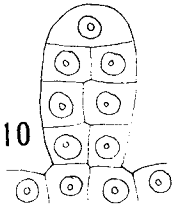
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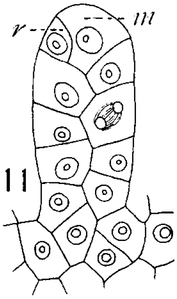
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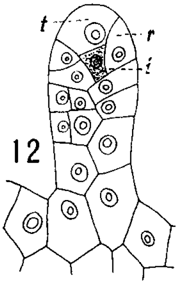
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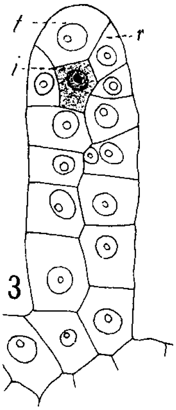
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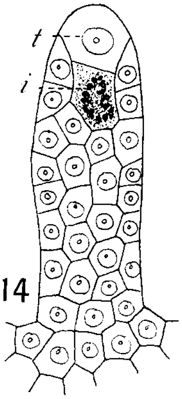
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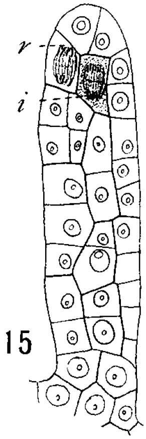
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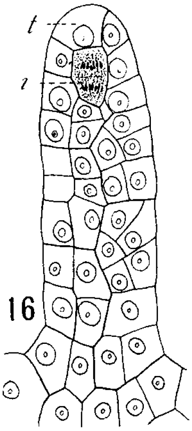
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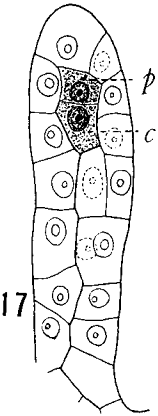
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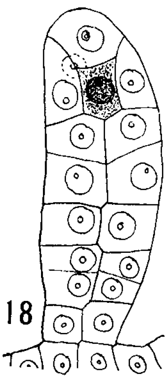
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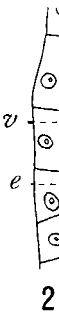
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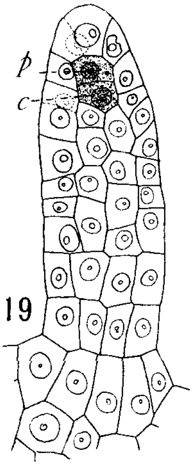
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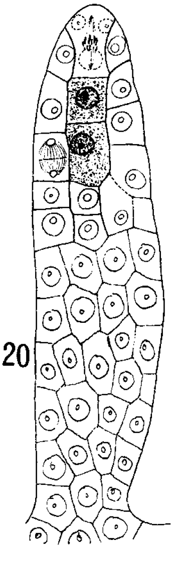
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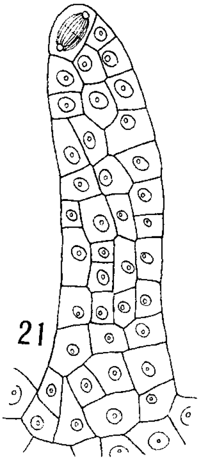
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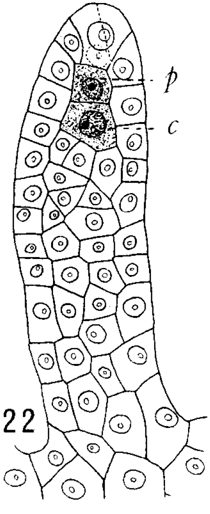
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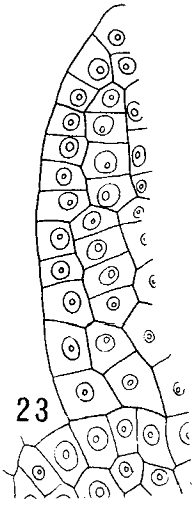
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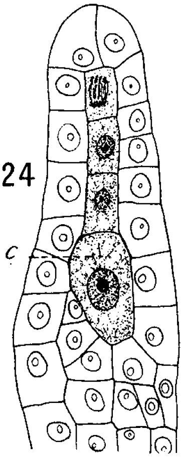

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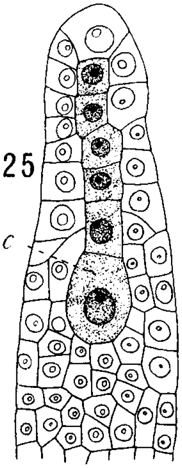

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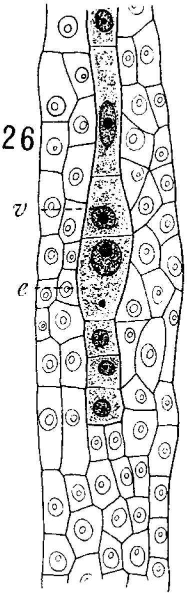

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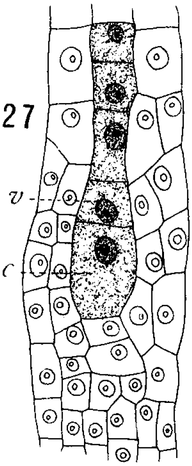

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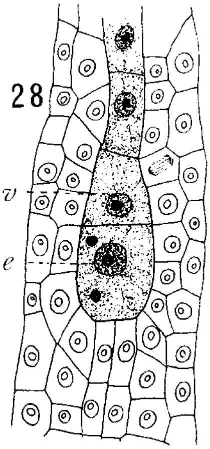

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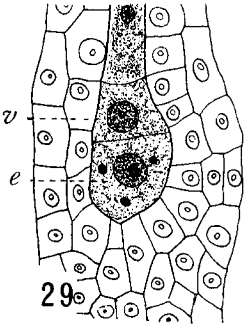

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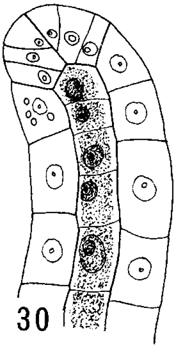

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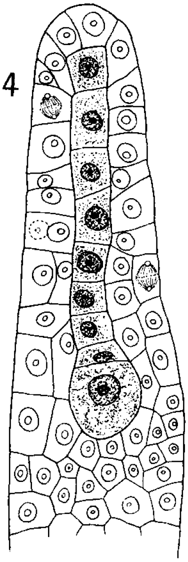

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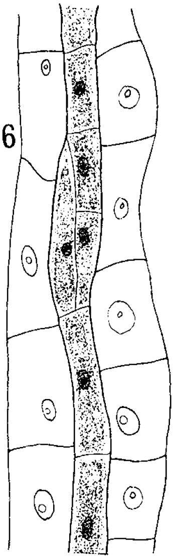

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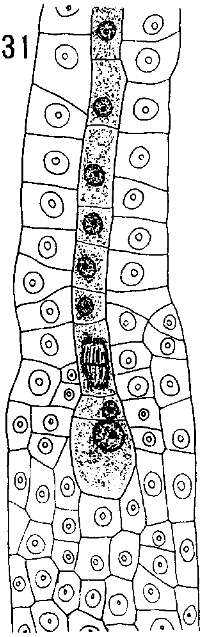

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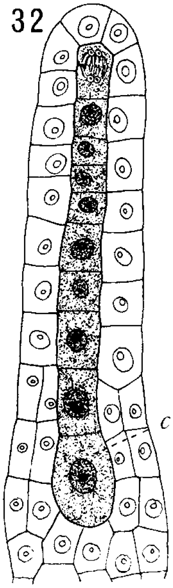

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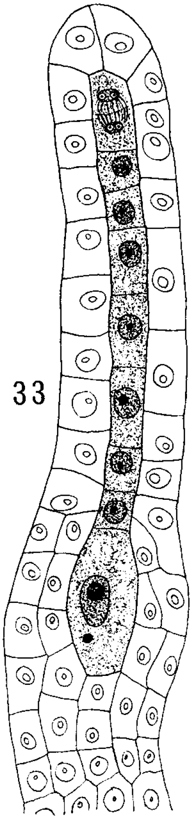

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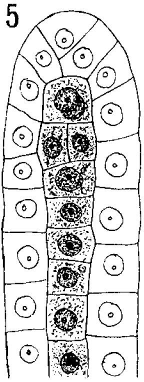

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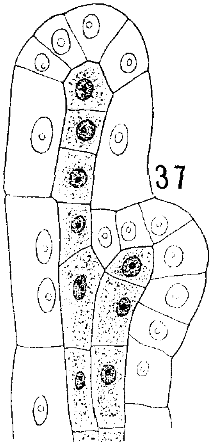

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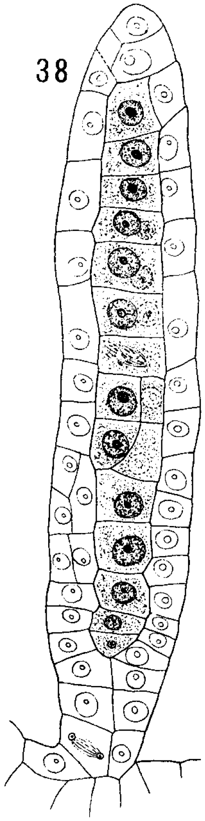

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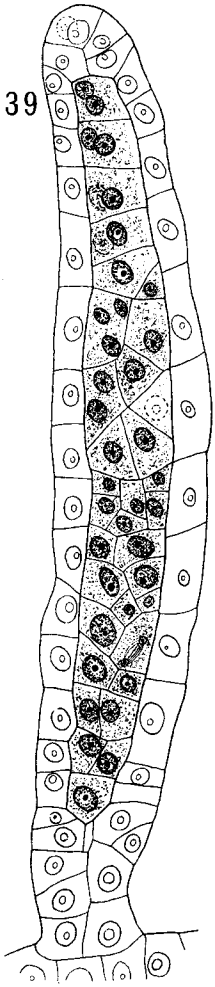

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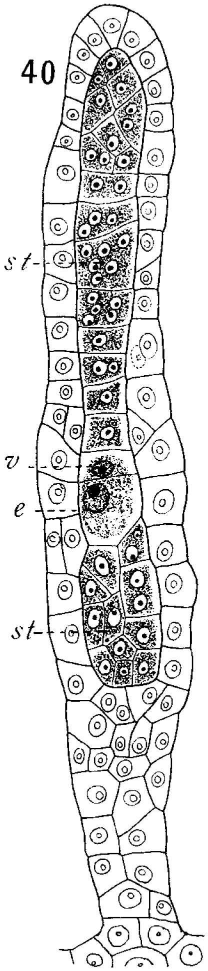

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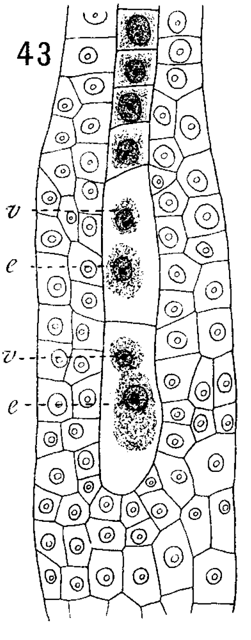

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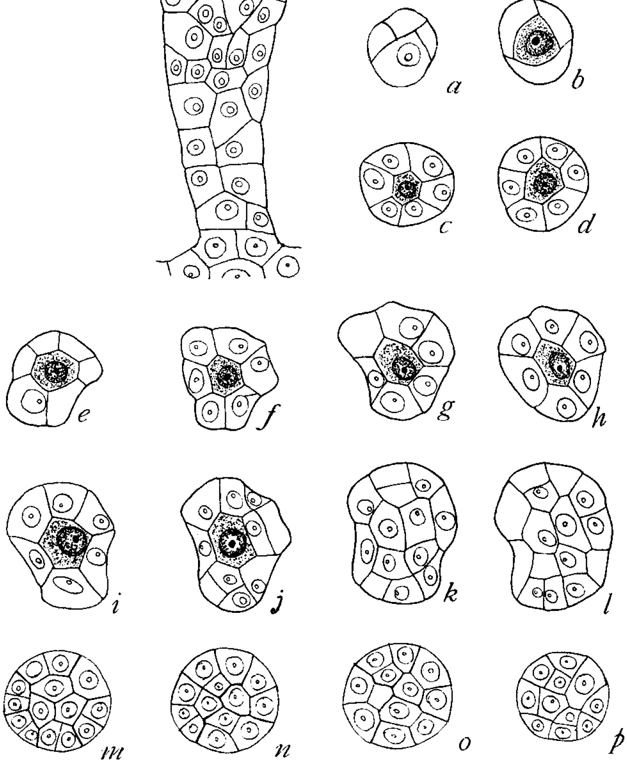

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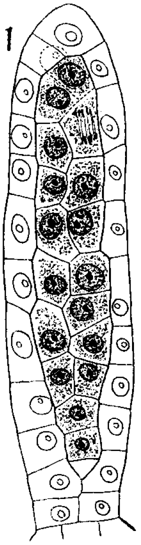

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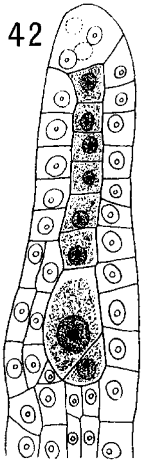

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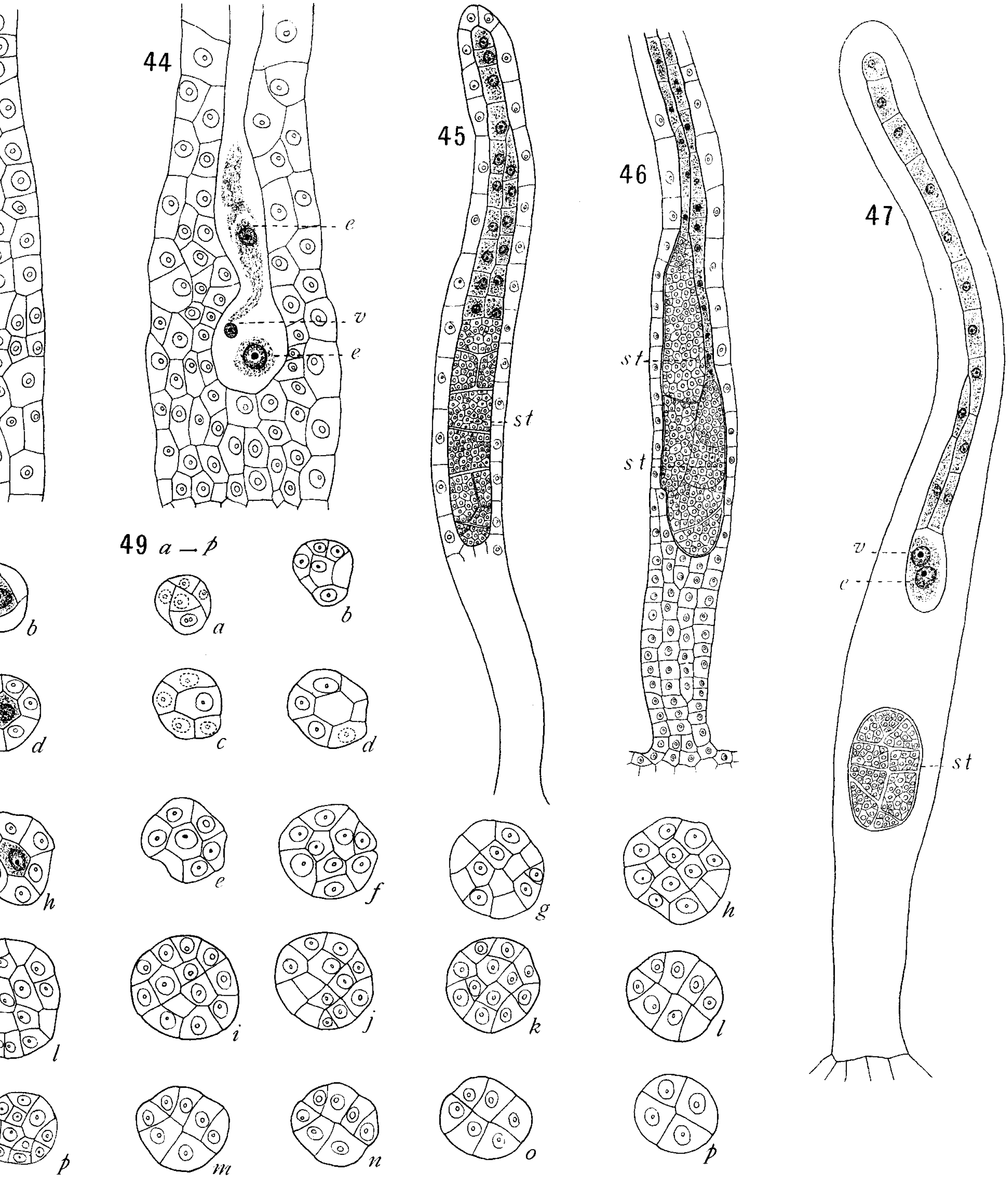

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FIG. 24. Archegonium showing division of third canal initial and rapid increase in size of the central cell; basal work of terminal cell apparently closed.

FIG. 25. Archegonium showing axial row affected by method of peripheral segment cutting (see *fig. 23*); work of terminal cell not finished; venter double walled, pedicel very massive.

FIGS. 26–29. Venters after recent division of the central cells; eggs and ventral canal cells of nearly equal size; egg cells showing masses of chromatin thrown off into the cytoplasm — an occurrence quite common for eggs, less so for ventral canal cells; evidences of a row below the egg in *figs. 26–28.*

FIG. 30. Tip of a mature archegonium, showing that last divisions in both neck and axial row have been intercalary.

FIG. 31. Venter with egg and ventral canal cell; lowest canal cell dividing showing that intercalary growth takes place after the cutting off of the ventral canal cell.

FIGS. 32–33. Young archegonia with remarkably large canal cells; central cells not yet divided; intercalary divisions taking place in last cells of the axial rows; both mitotic figures show bodies resembling centrospheres; basal segment cutting of apical cells completed.

FIG. 34. Egg and ventral canal cell, and seven canal cells; no division of central cell found earlier; upper canal cell appears to be produced by the terminal cell; longitudinal division of terminal cell prevents further basal segment cutting; intercalary growth of neck in progress as shown by mitotic figures; venter double-walled to an unusual distance above the egg.

FIG. 35. Young archegonium slightly abnormal, showing beginning of two axial rows near apex.

FIG. 36. Part of neck of an old archegonium, showing two axial rows for a short distance.

FIG. 37. Tip of an abnormal archegonium having two axial rows, each with its own apex and apical cell.

FIG. 38. Young antheridium modified by the possession of archegonium characters; the members of an evident axial row are separated by transverse walls; these cells dividing to form two rows; the double wall in the lower part and the two undivided large cells opposite to it are indications that this specimen might have produced a bisexual organ of the nature of that shown in *fig. 40.*

FIG. 39. Young antheridium further advanced; the double axial row with transverse walls are archegonium characters.

FIG. 40. A bisexual organ with evident archegonial and antheridial characters; the egg, ventral canal cell, and adjacent canal cells; the divisions to form a double-walled venter; the elongated pedicel and the terminal cell are undoubted archegonial characters; the oblique and irregular primary

walls and the spermatogenous tissue are antheridial characters; several similar organs were found.

FIG. 41. A young normal antheridium; in mature antheridia distinct regions of spermatogenous tissue can be detected representing each of these primary cells.

FIG. 42. A young archegonium with a cell cut from the lower part of central cell; whether the larger cell represents the ventral canal cell and the smaller one the egg could not be definitely determined.

FIG. 43. A venter containing two eggs and two ventral canal cells; whether the upper cell is the lowest canal cell divided or the original ventral canal cell divided could not be determined.

FIG. 44. A double venter with two eggs; all cross walls have disappeared.

FIGS. 45–46. Abnormal antheridia; in each case the mass of spermatogenous tissue is separated by the primary walls into distinct regions characteristic of antheridia; each organ has an outlet of two axial rows which before reaching the apex becomes one row; in *fig. 46* there are two masses of sperm tissue, each with its own axial outlet; the pedicels and necks are distinctly archegonial characters.

FIG. 47. A modified archegonium with traces of two axial rows, and a mass of sperm mother-cells developing in the elongated pedicel.

FIG. 48, *a–p*. Cross-sections of an archegonium from the terminal cell to the lower part of the pedicel; the middle cell and the three peripheral cells cut from it shown in *b;* the central cell and double wall of venter are shown in *j;* and the quadrate character of the pedicel in *n* and *o*.

FIG. 49, *a–p*. Cross-sections of an archegonium from terminal cell to base of pedicel; the massive character of pedicel shown in *f–i;* the four basal cells not divided (*p*).